

DIVERSITY AMONG GROUND-DWELLING SPIDER ASSEMBLAGES: HABITAT GENERALISTS AND SPECIALISTS

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ABSTRACT. We sampled assemblages of ground-dwelling spiders with pitfall traps in six terrestrial habitats representing a successional gradient in southwestern Virginia, during the summer of 2002. Approximately half of the 50 species trapped were habitat specialists with low abundance, found at only one of the sites, which is qualitatively consistent with the literature. Only four species, *Schizocosa ocreata* (Hentz 1844), *Pirata insularis* (Emerton 1885) *Pirata aspirans* (Chamberlain 1904) and *Neoantistea magna* (Keyserling 1887) were found at as many as four sites. A few species that were found in more than one study from disparate geographical communities, such as *Trochosa terricola* (Thorell 1856) tended also to be relatively abundant habitat generalists. In general, the majority of spider species found in studies such as ours that examined multiple sites were habitat specialists and had low abundance. For our sample sites, there was no relationship between any measure of spider diversity (S , H' , J') and successional age. Our results, and those of most other published studies, are consistent with the hypothesis that spider assemblages do not undergo succession and except for a few very common generalist species the composition of these communities is unpredictable, and may depend more on stochastic colonization and specific resource requirements of specialists following immigration than on any predictable association with successional parameters.

Keywords: Cursorial spiders, habitat specialization, spider diversity, succession

The importance of predators in the structure and function of natural ecosystems is becoming increasingly well documented (Terborgh et al. 2001). Spiders are widespread and diverse predators that are part of terrestrial arthropod assemblages (Wise 1993) and arthropods comprise more than half of known species (Wilson 1992). Cursorial spiders in particular are the dominant arthropod predators in many terrestrial communities, e.g., grasslands (Weeks & Holtzer 2000) and forest floor litter (Uetz 1979). Their position in trophic structure of communities often is complex: spiders in forest litter belong to both the decomposition and the grazing food webs because they consume detritivores/fungivores and herbivores (Uetz 1975; Wise et al. 1999). As larger species of wolf spiders mature, they prey more on herbivores that are part of the grazing food web (Uetz 1975; McNabb et al. 2001). Spiders have been experimentally demonstrated to exert important effects on the populations of other arthropods in a variety of experimental systems, including agricultural,

old field, and forest litter communities (Hurd & Eisenberg 1990; Riechert & Bishop 1990; Moran et al. 1996; Lawrence & Wise 2000).

Given their demonstrated importance to the structure and function of many communities, it is important to gather information on the distribution and abundance of cursorial spider species. Often it has been difficult to determine what features of an environment determine which, or how many, species of cursorial spiders will be present. For example, spider diversity may not follow a trend toward increasing diversity with increasing successional age (Hurd & Fagan 1992; Aitchison & Sutherland 2000; Buddle et al. 2000) that has been a traditional expectation for species of plants and animals during terrestrial succession (Odum 1969).

Spiders have legendary powers of dispersal and often are among the first colonizers of disturbed sites (Hodkinson et al. 2001); the first known colonist of Krakatoa was a spider (Spiller et al. 1998). Many spiders have the ability to disperse by “ballooning” with silk at some point in their life cycles (Hodkinson et al. 2001). Lycosids and gnaphosids balloon

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Figure 1.—Map of the Science Park on the campus of Washington & Lee University. The habitats used for sampling sites are described in the text: CG = cedar grove; OF = old field; DR = disturbance recovery; LH = lowland hardwoods; UH = upland hardwoods; PW = Pine woods.

as juveniles, while many linyphiids retain the capability throughout adulthood (Mrzljak & Wiegleb 2000). However adept they are at initially getting to new sites, cursorial spiders should have specific habitat preferences that dictate which species will become established and how abundant they will be. Some species are more particular than others: along a successional gradient in Delaware, the lycosid *Pirata insularis* (Emerton 1885) was found abundantly in all four communities examined, whereas the gnaphosid *Zelotes hentzi* (Barrows 1945) was rare and confined to the youngest successional site (Hurd & Fagan 1992). The structure of vegetation and some physico-chemical habitat parameters may determine a spider's habitat choice (Mrzljak & Wiegleb 2000). Along forest litter gradients and in agroecosystems, lycosids manifest microhabitat preferences possibly based upon leaf litter, herbaceous vegetation and available moisture (Weeks & Holtzer 2000). The question of what determines the structure of cursorial spi-

der guilds is far from being answered, and will require the accumulation of much more data (Uetz et al. 1999).

We report here on a field study in which six field sites, representing different successional seres, are compared with respect to ground-dwelling spider species captured by pitfall trap sampling. We compared diversity among sites, and the extent of habitat specialization (relative number of habitats in which species were found in this, and in previous studies) in these spiders.

METHODS

Study Sites.—The study sites we used for this study are located in the 35ha Science Park of Washington & Lee University in Rockbridge Co, Virginia, USA (Fig. 1). The sites were chosen to represent different habitat types and stages of secondary terrestrial succession typical of this region, as described below in order of successional age.

1. *Disturbance recovery (DR)*: This site is

a 0.5ha patch of level ground, surrounded by woods, that is being used in a long-term study of community succession. The ground had been stripped of all native top soil prior to 2001, leaving a bare, hard clay surface. During fall and winter 2001 ground leaf mulch was applied to the bare clay and tilled into the upper 2–3cm, after which seeds of 19 native forb species and five native grasses were planted. The plant assemblage that sprouted during spring and summer 2002 constituted a dense mixture of these intentionally planted species and incidental species that were present as seed in the mulch (an especially conspicuous member of the second category during late summer was ragweed, *Ambrosia artemisiifolia*). The vegetation, which reached a height of approximately 0.5m, was dense enough to provide shade at the soil surface. There was no organic litter layer on the soil, owing to the absence of plants on the site during the previous year. This site is surrounded by a wire fence to keep out deer, and is surrounded by woods.

2. *Old-field (OF)*: This site is a third year successional sere, which was previously subjected to mowing once or twice annually. It is fully open to the sun, and consists of grasses and forbs growing up to approximately 0.5m high typical of early successional old-fields in this region, including patches of emergent (ca 1.5m high) late-season goldenrod (*Solidago* spp.), teasel (*Dipsacus sylvestris*), and ragweed (*Ambrosia artemisiifolia*). Plant height and soil shading at this site were similar to those at site *DR* (see above), but here there was a sparse and shallow (≤ 0.5 cm depth) litter layer consisting of dead plant stalks and leaves from the previous year's growth. An abundant and diverse arthropod assemblage inhabits this site, the most conspicuous of which are several species of grasshoppers (Acrididae). The cedar grove site (*CG*, see below) forms the western border of the old-field site.

3. *Cedar grove (CG)*: This site consists of a near monoculture of 6–8m high eastern red cedar (*Juniperus communis*) from 30–40 years old, with a sparse understory of hardwood saplings and very little herbaceous ground cover. In our geographical area, cedars grow in old-fields until they shade out herbaceous vegetation, and then may dominate the community until they senesce and are re-

placed by hardwoods. The ground is mostly in shade, with small patches of sunlight most of the day. The soil is sandy and well-drained. The litter layer consists of a ≤ 1.0 cm layer of dead cedar needles. We considered this site to be the earliest forest community, between *OF* and *PW* in age.

4. *Pine woods (PW)*: This site is in deep shade, provided by an overstory of tall (≥ 10 m) white pines (*Pinus strobus*) and mixed species of smaller hardwoods, especially red maple (*Acer rubrum*) and white ash (*Fraxinus americana*), with an understory of saplings and shrubs. This species mix represents an alternative intermediate stage of succession to the assemblage in *CG*; the relative height of the hardwoods in this stand indicated that *PW* may be the older of the two, at least 40 years old. The site is located on a flood plain, with relatively moist soil. The litter layer is mainly dead needles, but somewhat thicker (≥ 1 cm).

5. *Upland hardwoods (UH)*: This site is within the woodlot boundary of the *DR* site. The overstory is of mixed hardwoods 10–15m high, especially white ash and tulip poplar (*Liriodendron tulipifera*), with several species of oaks (*Quercus* spp.), and red maple in the understory. This species mix is typical of the community that replaces coniferous species, i.e., perhaps 10–15 years older than site *PW* (i.e., 50–55 years old). The soil here is well-drained and rich in organic matter, with a relatively deep (3–4cm) leaf litter layer.

6. *Lowland hardwoods (LH)*: This is a mature hardwood forest that has been subjected to little disturbance for at least the past 70 years, with canopy trees (tulip, maple, white ash, and mixed oak) ≥ 30 m. This site is deeply shaded and is on a floodplain at the bottom of a slope, downward from site *UH*. The leaf litter is more compacted than and not as thick as at site *UH*, probably because of the increased soil moisture and humidity.

Sampling.—We sampled ground-dwelling spiders at each site with six pitfall traps set out in a 2×3 array, such that no trap was closer than approximately 1.5m from its nearest neighbor. Trap arrays were at least 10m from the edge of the habitats they sampled. Each trap consisted of a 10cm diameter, 11cm deep polypropylene cup fitted into a permanent sleeve that was sunk into the ground flush with the soil surface. A cover for each

Table 1.—Total numbers of cursorial spiders by habitat type (sampling site): DR = disturbance recovery; OF = old field; CG = cedar grove; PW = pine woods; UH = upland hardwoods; LH = lowland hardwoods. Superscripts denote other studies in which species were found: 1 = Hurd & Fagan (1992); 2 = Buddle et al. (2000); 3 = Aitcheson & Sutherland (2000); 4 = Bonte et al. (2002); 5 = Gajdos & Toft (2000); 6 = Uetz (1975); 7 = Uetz (1976); 8 = Uetz (1977); 9 = Uetz (1979); 10 = Buddle and Rypstra (2003); and 11 = Draney (1997). Nomenclature follows Platnick (2003).

Family	Genus;species	DR Total	OF Total	CG Total	PW Total	UH Total	LH Total	Species Total
Agelenidae Koch 1837	<i>Agelenopsis pennsylvanica</i> ¹ Koch 1843						3	3
Antrodiaetidae Gertsch 1940	<i>Antrodiaetus unicolor</i> Hentz 1842			1	1			2
Corinnidae Karsch 1880	<i>Castianeira cingulata</i> ^{1, 6, 8, 9, 11} Koch 1841					1		1
	<i>Castianeira longipalpus</i> ^{1, 6, 7, 8, 9, 11} Hentz 1847					1	3	4
	<i>Phrurotimpus alarius</i> ^{1, 6, 8, 9} Hentz 1847			2		4	16	22
	<i>Phrurotimpus borealis</i> ^{3, 6, 9} Emerton 1911					3	2	5
	<i>Phrurotimpus minutus</i> ^{1, 6} Banks 1892					1	1	2
	<i>Phrurotimpus sp.</i> Chamberlin & Ivie 1935					1	1	2
	<i>Scotinella britcheri</i> Petrunkevitch 1910		1					1
	<i>Scotinella formica</i> ¹ Banks 1911	1	8					9
	<i>Scotinella sp.</i> Banks 1911						1	1
Cybaeidae Banks 1892	<i>Cybaeus sp.</i> Koch 1868				3	1	1	5
Dysderidae Koch 1837	<i>Dysdera crocata</i> ⁴ Koch 1838		1					1
Gnaphosidae Pocock 1898	<i>Drassyllus depressus</i> Emerton 1890		1					1
Hahniidae Bertkau 1878	<i>Hahnina cinerea</i> ^{3, 9} Emerton 1890			1		5		6
	<i>Antistea brunea</i> Emerton 1909				1	1		2
	<i>Hahnidae sp. 1</i>					1	3	4
	<i>Neoantistea agilis</i> ^{3, 11} Keyserling 1887		1	1				2
	<i>Neoantistea magna</i> Keyserling 1887		1	1	1	1		4
Linyphiidae Blackwall 1859	<i>Drapetisca alteranda</i> Chamberlin 1909				1			1
Subfamily: Linyphiinae	<i>Stemonyphantes lineatus</i> Linnaeus 1758		1					1
	<i>Tenuiphantes zebra</i> Emerton 1882					1		1
Lycosidae Sundevall 1833	<i>Allocosa funerea</i> ^{1, 11} Hentz 1844	2	1					3
	<i>Allopecosa aculeata</i> Clerck 1757	1						1
	<i>Arctosa virgo</i> Chamberlin 1925			1				1
	<i>Hogna helluo</i> ^{1, 6, 10} Walckenaer 1837		1	1				2
	<i>Pardosa distincta</i> ¹ Blackwall 1846	2	1					3
	<i>Pardosa milvina</i> ^{1, 10, 11} Hentz 1844	11						11
	<i>Pardosa saxatilis</i> ^{1, 6} Hentz 1844	16						16
	<i>Pardosa sp. 1</i> Koch 1847				1			1
	<i>Pardosa sp. 2</i> Koch 1847	7						7
	<i>Pirata aspirans</i> ^{1, 6} Chamberlin 1904	1	2		1		2	6

Table 1.—Continued.

Family	Genus;species	DR Total	OF Total	CG Total	PW Total	UH Total	LH Total	Species Total
Lycosidae Sundevall 1833	<i>Pirata insularis</i> ^{1, 3, 6} Emerton 1885			25	37	1	141	204
	<i>Rabidosa rabida</i> ^{1, 11} Walckanaer 1837		5					5
	<i>Schizocosa avida</i> ¹ Walckanaer 1837	3	4					7
	<i>Schizocosa bilineata</i> ^{1, 11} Emerton 1885		2					2
	<i>Schizocosa ocreata</i> ^{1, 6, 7, 8, 11} Hentz 1844			6	1	5	3	15
	<i>Trochosa terricola</i> ^{1, 2, 3, 4, 5} Tho- rell 1856	2	1					3
	<i>Trochosa</i> sp Kock 1847					1		1
Oonopidae Simon 1890	<i>Orchestina saltitans</i> Banks 1894	1						1
Oxyopidae Thorell 1870	<i>Oxyopes salticus</i> ^{1, 11} Hentz 1845		2					2
Philodromidae Thorell 1870	<i>Thanatus formicinus</i> ¹¹ Clerck 1757		1					1
Pisauridae Simon 1890	<i>Dolomedes tenebrosus</i> Hentz 1844	1					1	2
Salticidae Blackwall 1841	<i>Habronattus borealis</i> Banks 1895	1						1
	<i>Neon nelii</i> ³ Peckham & Peckham 1888	1				1		2
Theridiidae Sundevall 1833	<i>Euryopsis argentea</i> Emerton 1882					1		1
Thomisidae Sundevall 1833	<i>Ozyptila</i> sp. Simon 1864		1					1
	<i>Xysticus ferox</i> ^{1, 7, 9, 11} Hentz 1847			1		1		2
	<i>Xysticus punctatus</i> Keyserling 1880							0
	<i>Xysticus</i> sp. Koch 1835			1				1
Habitat Total Abundance =		50	35	41	47	31	178	382

trap was constructed using a Petri dish lid with nails to elevate it 3cm above the lip of the trap. These covers kept out rainwater and falling debris. Sampling occurred at weekly intervals from early June to mid-August, and then once at the end of September 2002 (total = 354 trap-days). Each time we sampled, we put approximately 2cm of 70% ethanol into each trap during the afternoon (ca 1600h), and collected the samples 16–18h later.

All adult spiders collected from the traps were counted and identified using taxonomic keys (Kaston 1978, 1981; online taxonomic updates <http://kaston.transy.edu/spiderlist/Kaston78.htm> and <http://kaston.transy.edu/spiderlist/kast.htm>; Roth 1993). Our nomenclature follows Platnick (2003). We did not attempt to enumerate or identify to species spiders in the subfamily Erigoninae (family

Linyphiidae), which were infrequently captured, and most of which were represented by a single individual. At least one individual of each species collected (a male and female of each, when available) was preserved in Kahle's fluid as part of a reference collection.

As with any field study in a diverse species assemblage, sampling efficacy is not likely to be equal among taxa. In the case of pitfall traps, for instance, the most active spiders (e.g., many lycosids) may have a tendency to be disproportionately sampled relative to more sedentary species (e.g., clubionids). Therefore, species richness and relative abundance of captured spiders may not accurately reflect the entire resident assemblage, but can be used for comparisons among sites of those taxa that are susceptible to pitfall trapping.

Data analysis.—We compared sampling

Table 2.—The number of shared cursorial species between habitats, and species diversity (richness = S ; J' = evenness; Shannon's diversity = H') for each habitat based on pit trap samples. Sites arranged in order of increasing successional age from left to right and top to bottom. Site descriptions given in Methods.

Sites:	DR	OF	CG	PW	UH	LH
DR	14	—	—	—	—	—
OF	6	18	—	—	—	—
CG	0	3	12	—	—	—
PW	1	2	4	9	—	—
UH	1	1	6	5	18	—
LH	2	1	3	4	9	13
H' =	2.06	2.57	1.45	0.94	2.63	0.96
S =	14	18	12	9	18	13
J' =	0.78	0.89	0.58	0.43	0.91	0.37

sites with regard to diversity, measured as (1) the number of species found, or species richness, S , (2) Evenness of distribution of individuals among species, J' , and (3) Shannon's diversity, H' , which is a measure of the interaction between evenness and richness (Pielou 1969; Hill 1973).

RESULTS

We collected a total of 50 species of ground-dwelling spiders from our six sampling sites (Table 1). Twenty-six of these were habitat specialists, found at only one site; no species was found at all six sites. The spiders with the broadest distribution, found at four of the six sites, were the lycosids *Schizocosa ocreata*, *Pirata insularis*, *Pirata arenicola* and the hahniid *Neoantistea magna*. Both *S. ocreata* and *P. insularis* were found at all four wooded sites and none was collected at either of the open field sites. However, *P. arenicola* and *N. magna* were found at combinations of wooded and open field sites.

Some of the spiders we found appear to have wide geographical distributions. Five species in Table 1 were also reported in four or more other studies from Denmark, Belgium and Manitoba, as well as sites in the U. S. (Delaware, Ohio, Georgia and Virginia). However, there appears to be no reliable relationship between how broadly cursorial spider species are distributed among geographic sites, how many sites they occupy within a study, or what kind of habitat (e.g., wooded or open) they prefer in those studies that sampled more than one habitat type.

We found no relationship between successional age and any measure of diversity (Table

2). The pine stand (PW), representing the intermediate stage of succession, had the lowest spider diversity (Table 2). This site also had the lowest apparent vegetational diversity among the six sites: there was almost no ground cover vegetation, and the tree diversity was limited to white pine and a few small deciduous saplings. However, there were no other apparent correlative trends between spider diversity and site structure. The highest H' diversity and J' evenness values we found were in the nearly mature forest (UH), and the old field (OF), our second to youngest site, yielding virtually identical rank abundance patterns (Fig. 2). Although species richness was the same (18) for both of these sites, they only shared a single species, *N. magna* (Table 2). The climax forest (LH) had the lowest H' value even though species richness was about average among the sites. This was because of the high dominance of a single species (*Pirata insularis*), which was reflected by the low value of J' (Tables 1 & 2).

Our most abundant species trapped was *P. insularis*, accounting for more than half of all spiders trapped (Table 1). The abundance of *P. insularis* in our traps was highest in mid-June, decreasing to just two individuals caught in August and September. From the beginning of the sample season, the sex ratio of this species was highly male-biased. As the season progressed it shifted to a female-biased ratio. July appeared to be the month of reproduction: females were caught with egg sacs on 2 July, and with juveniles riding on the dorsa of their abdomens on 10 and 19 July.

We also were able to record some repro-

ductive data for *S. ocreata* and *P. saxatilis*. On 1 July we found a female *S. ocreata* with a new (white) egg case. On 10 July a female with a gray (older) egg case was captured. The case was dissected and almost fully developed eggs were found inside, with fangs evident. On 19 July a female was caught with juveniles on her back. On 20 June we found a female *P. saxatilis*, with an egg case. On two other occasions (2 and 17 July) we found females with egg cases. On 26 July we found one with spiderlings on her dorsum, and brought it back to the lab for observation. On 29 July spiderlings were seen leaving the mother's dorsum and by 30 July they had all dispersed.

DISCUSSION

As with previously reported studies, we found that most ground-dwelling spider species were habitat specialists, found at one or two sites, and very few were generalists. Because rare species may be present in such low numbers that they may be missed by sampling, we cannot conclude that a species that did not show up in our samples was completely absent from a given site, but we can at least score a species as present if we captured it in a sample. This is a problem common among studies that report the presence of rare species, many of which are represented by a single trapped individual (e.g., 31 of 105 species reported by Buddle et al. 2000).

Both Aitchison & Sutherland (2000) and Hurd & Fagan (1992) found only three species that occupied four or more sites; we found only four species in that category. However, very few of these are the same species. Six of the species we found were also reported from these two studies in Manitoba, one of which (*Trochosa terricola*) was found in both Manitoba studies and in our present study (Table 1) and has been reported to occur from as far away as Finland (Aitchison & Sutherland 2000) and Belgium (Bonte et al. 2002). Not surprisingly, there were more spider species (20) in common between our present study and the geographically closer Delaware sites of Hurd & Fagan (1992). The most abundant species in both the present Virginia study and the Delaware study was the lycosid, *Pirata in-sularis*.

The majority of spiders we encountered belonged to the family Lycosidae. While *P. in-sularis* preferred wooded sites, the next two

most abundant lycosids (*Pardosa milvina* and *P. saxatilis*) were confined to the most open site (DR). Buddle & Rypstra (2003) also noted that *Pardosa* species achieve dense populations in barren exposed habitats. *Schizocosa ocreata* was found in all four wooded sites. This species is commonly found in leaf litter of deciduous forests in eastern North America (Wagner & Wise 1996). Uetz (1977) noted that *S. ocreata* occurs in simple litter where the leaves are compressed and the ground is relatively moist.

The diversity of sampled spiders in our study did not follow a successional gradient, a finding of other studies as well: a forest successional gradient in Delaware (Hurd & Fagan 1992), and forests in Manitoba (Aitchison & Sutherland 2000; Buddle et al. 2000). Part of the difficulty may lie in the relative scarcity of studies that examine a wide range of successional seres at a given locale. In any event, attempting to find predictable environmental correlates to spider diversity have proved frustrating for many researchers. In their 20 year study of coastal dunes Gajdos & Toft (2000) found that temporal changes in community composition were greater than differences occurring between habitats. It was impossible for them to determine what ways ecological characteristics changed for those spider species in which abundance changed over time. Differences in the physical structure of leaf litter and its complexity can influence species composition, spider abundance and diversity generally increasing with increased litter depth in some studies (Uetz 1975, 1977, 1979; Buddle & Rypstra 2003). Uetz (1975) found that weather patterns, which could be tied to prey productivity for spiders, did not correlate significantly to any diversity measure. Instead, he found that richness and evenness were related to litter depth, and moderately well related to successional age and plant cover. However, in our study we found as many spider species in the two open habitats with almost no litter (DR and OF) as we did in the two hardwood forest habitats (UH and LH). Mrzljak & Wiegler (2000) presented evidence that species richness and abundance are limited by vegetative stratification and height, e.g., tall grass stands had more species than short grass stands. Hurd & Fagan's (1992) study of spider assemblages in Delaware found the main difference to be between

woodland and open habitats and not age of the habitats: diversity of cursorial spiders generally was greater in open field habitats than in woodlands. However, in our present study we found no clear difference among sites based on presence, absence, or extent of tree cover.

It is apparently not difficult to predict the presence in spider assemblages of some very broad generalists such as *Trochosa terricola*, but for most habitat specialists, such prediction is problematic. Given the data so far, it is hard to refute the null hypothesis that spider diversity within a site may be more a function of stochastic colonization opportunities of different species rather than a set of intra-community assembly rules (*sensu* Diamond 1975). Other factors that can influence species membership in arthropod assemblages, including spiders, are habitat features such as area, degree of isolation, and movement patterns of animals relative to their resource requirements (Matter 1996, 2000; Hanski 1999; Marshall et al. 2000; Samu et al. 2003). Thus, changing spider community composition over time is not really true succession at all, but rather repeated colonization by opportunistic species. The success of such colonists, once they invade a habitat, may well depend on competitive abilities (Marshall et al. 2000) and the changing environmental conditions that accompany plant succession (Mrzljak & Wiegand 2000; Hodkinson et al. 2001), but as yet we are far from being able to predict cursorial spider composition among seres with any degree of precision.

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LITERATURE CITED

- Aitchison, C.W. & G.D. Sutherland. 2000. Diversity of forest upland arachnid communities in Manitoba taiga (Araneae, Opiliones). *Canadian Field Naturalist* 114:636–651.
- Bonte, D., L. Baert & J.P. Maelfait. 2002. Spider assemblage structure and stability in a heterogeneous coastal dune system (Belgium). *Journal of Arachnology* 30:331–343.
- Buddle, C.M. & A.L. Rypstra. 2003. Factors initiating emigration of two wolf spider species (Araneae: Lycosidae) in an agroecosystem. *Environmental Entomology* 32:88–95.
- Buddle, C.M., J.R. Spence & D.W. Langor. 2000. Succession of boreal forest spider assemblages following wildfire and harvesting. *Ecography* 23: 424–436.
- Diamond, J.M. 1975. Assembly of species communities. Pp. 342–444. *In* *Ecology and Evolution of Communities* (M.L. Cody and J.M. Diamond, eds.). Belknap Press, Massachusetts.
- Draney, M.L. 1997. Ground-layer species (Araneae) of a Georgia piedmont flood plain agroecosystem: species list, phenology and habitat selection. *Journal of Arachnology* 25:333–351.
- Gajdos, P. & S. Toft. 2000. A twenty-year comparison of epigeic spider communities (Araneae) of Danish coastal heath habitats. *Journal of Arachnology* 28:90–96.
- Hanski, I.A. 1999. *Metapopulation Ecology*. Oxford University Press, Oxford, U.K.
- Hill, M.O. 1973. Diversity and evenness: a unifying notion and its consequences. *Ecology* 54:427–432.
- Hodkinson, I.D., S.J. Coulson, J. Harrison & N.R. Webb. 2001. What a wonderful web they weave: spiders, nutrient capture and early ecosystem development in the high Arctic—some counter-intuitive ideas on community assembly. *Oikos* 95: 349–352.
- Hurd, L.E. & R.M. Eisenberg. 1990. Arthropod community responses to manipulation of a bi-trophic predator guild. *Ecology* 71:2107–2114.
- Hurd, L.E. & W.F. Fagan. 1992. Cursorial spiders and succession: age or habitat structure? *Oecologia* 92:215–221.
- Kaston, B.J. 1978. *How to Know the Spiders*. Wm. C. Brown Company Publishers, Dubuque, Iowa.
- Kaston, B.J. 1981. *Spiders of Connecticut*. State Geological and Natural History Survey of Connecticut, Hartford, Connecticut.
- Lawrence, K.L. & D.H. Wise. 2000. Spider predation on forest-floor Collembola and evidence for indirect effects on decomposition. *Pedobiologia* 44:33–39.
- Marshall, S.D., S.E. Walker & A.L. Rypstra. 2000. A test for a differential colonization and competitive ability in two generalist predators. *Ecology* 81:3341–3349.
- Matter, S.F. 1996. Interpatch movement of the red milkweed beetle, *Tetraopes tetraophthalmus*: individual responses to patch size and isolation. *Oecologia* 105:447–453.
- Matter, S.F. 2000. The importance of the relationship between population density and habitat area. *Oikos* 89:613–619.
- McNabb, D.M., J. Halaj & D.H. Wise. 2001. Inferring trophic positions of generalist predators and their linkage to the detrital food web in agroeco-

- systems: a stable isotope analysis. *Pedobiologia* 45:289–297.
- Moran, M.D., T.P. Rooney & L.E. Hurd. 1996. Top-down cascade from a bitrophic predator in an old-field community. *Ecology* 77:2219–2227.
- Mrzljak, J. & G. Wiegand. 2000. Spider colonization of former brown coal mining areas—time or structure dependent? *Landscape & Urban Planning* 1:131–146.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science* 164:262–270.
- Pielou, E.C. 1969. *An Introduction to Mathematical Ecology*. Wiley, New York.
- Platnick, N.I. 2003. The world spider catalog, version 4.0. American Museum of Natural History, online at <http://research.amnh.org/entomology/spiders/catalog81-87/index.html>.
- Riechert, S.E. & L. Bishop. 1990. Prey control by an assemblage of generalist predators: spiders in garden test systems. *Ecology* 71:1441–1450.
- Roth, V.D. 1993. *Spider Genera of North America*. American Arachnological Society.
- Samu, E., A. Sziranyi & B. Kiss. 2003. Foraging in agricultural fields: local 'sit-and-move' strategy scales up to risk-averse habitat use in a wolf spider. *Animal Behaviour* 66:939–947.
- Spiller, D.A., J.B. Cosos & T.W. Schoener. 1998. Impact of a catastrophic hurricane on island populations. *Science* 281:695–697.
- Terborgh, J., L. Lopez, P. Nuñez, M. Rao, G. Shahabuddin, G. Orihuela, M. Riveros, R. Ascanio, G. H. Adler, T. D. Lambert & L. Balbas. 2001. Ecological meltdown in predator-free forest fragments. *Science* 294:1923–1926.
- Uetz, G.W. 1975. Temporal and spatial variation in species diversity of wandering spiders (Araneae) in deciduous forest litter. *Environmental Entomology* 4:719–724.
- Uetz, G.W. 1976. Pitfall trapping in ecological studies of wandering spiders. *Journal of Arachnology* 3:101–111.
- Uetz, G.W. 1977. Coexistence in a guild of wandering spiders. *Journal of Animal Ecology* 46:531–541.
- Uetz, G.W. 1979. The influence of variation in litter habitats on spider communities. *Oecologia* 40:29–42.
- Uetz, G.W., J. Halaj & A.B. Cady. 1999. Guild structure of spiders in major crops. *Journal of Arachnology* 27:270–280.
- Wagner, J.D. & D.H. Wise. 1996. Cannibalism regulates densities of young wolf spiders: evidence from field and laboratory experiments. *Ecology* 77:639–652.
- Weeks, Jr., R.D. & T.O. Holtzer. 2000. Habitat and season in structuring ground-dwelling spider (Araneae) communities in a shortgrass steppe ecosystem. *Environmental Entomology* 29:1164–1172.
- Wilson, E.O. 1992. *The Diversity of Life*. Harvard University Press, Cambridge.
- Wise, D.H. 1993. *Spiders in Ecological Webs*. Cambridge University Press, New York.
- Wise, D.H., W.E. Snyder & P. Tuntitbunpakul. 1999. Spiders in decomposition food webs of agroecosystems: theory and evidence. *Journal of Arachnology* 27:363–370.

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